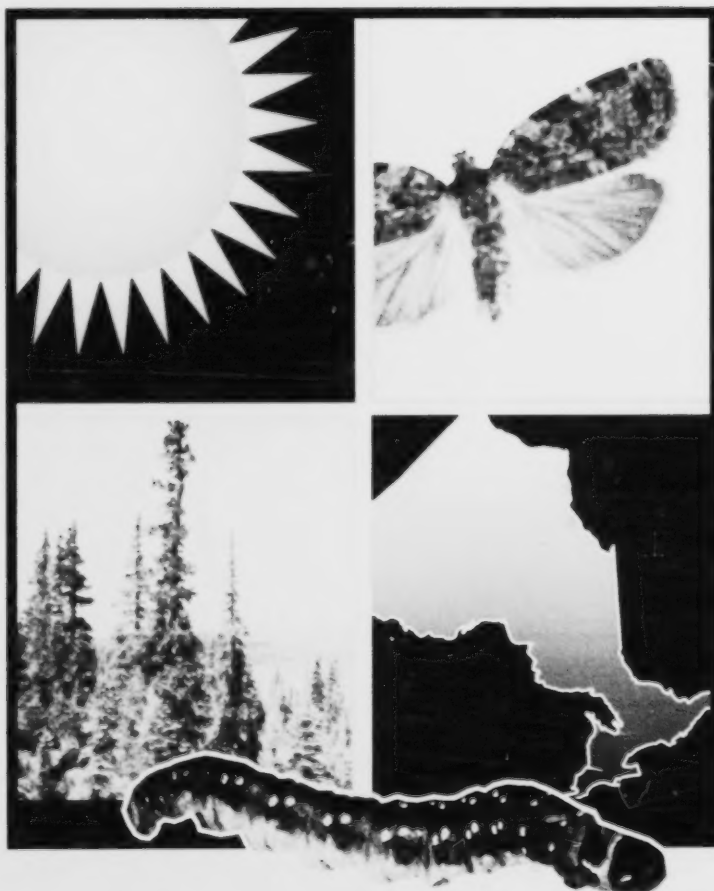13

ATMOSPHERE
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**Responding to
Climate Change
Through Partnership**

Ontario

Forecasting the Response to Climate Change of the Major Natural Biotic Disturbance Regime in Ontario's Forests:

the Spruce Budworm

Climate Change and MNR: A Program-Level Strategy and Action Plan

The following describes how the Ministry of Natural Resources works to contribute to the Ontario Government's commitment to reduce the rate of global warming and the impacts associated with climate change. The framework contains strategies and sub-strategies organized according to the need to understand climate change, mitigate the impacts of rapid climate change, and help Ontarians adapt to climate change:

Theme 1: Understand Climate Change

Strategy #1: Gather and use knowledge in support of informed decision-making about climate change. Data and information gathering and management programs (e.g., research, inventory, monitoring, and assessment) that advances our knowledge of ecospheric function and related factors and forces such as climate change are critical to informed decision-making. Accordingly, MNR will work to:

- Strategy 1.A: Develop a provincial capability to describe, predict, and assess the important short- (0-5 years), medium- (5-20 years), and long-term (20+ years) impacts of climate change on the province's ecosystems and natural resources.
- Strategy 1.B: Model the carbon cycle.

Strategy #2: Use meaningful spatial and temporal frameworks to manage for climate change. A meaningful spatial and temporal context in which to manage human activity in the ecosphere and address climate change issues requires that MNR continue to define and describe Ontario's ecosystems in-space and time. In addition, MNR will use the administrative and thematic spatial units required to manage climate change issues.

Theme 2: Mitigate the Impacts of Climate Change

Strategy #3: Gather information about natural and cultural heritage values and ensure that this knowledge is used as part of the decision-making process established to manage for climate change impacts. MNR will continue to subscribe to a rational philosophy and corresponding suite of societal values that equip natural resource managers to take effective action in combating global warming and to help Ontarians adapt to the impacts of climate change.

Strategy #4: Use partnership to marshal a coordinated response to climate change. A comprehensive climate change program involves all sectors of society as partners and participants in decision-making processes. The Ministry of Natural Resources will work to ensure that its clients and partners are engaged.

Strategy #5: Ensure corporate culture and function work in support of efforts to combat rapid climate change. Institutional culture and function provide a "place" for natural resource managers to develop and/or sponsor proactive and integrated programs. The Ministry of Natural Resources will continue to provide a "home place" for the people engaged in the management of climate change issues.

Strategy #6: Establish on-site management programs designed to plan ecologically, manage carbon sinks, reduce greenhouse gas emissions, and develop tools and techniques that help mitigate the impacts of rapid climate change. On-site land use planning and management techniques must be designed to protect the ecological and social pieces, patterns, and processes. Accordingly, MNR will work to:

- Strategy 6.A: Plan ecologically.
- Strategy 6.B: Manage carbon sinks.
- Strategy 6.C: Reduce emissions.
- Strategy 6.D: Develop tools and techniques to mitigate the impacts of rapid climate change.

Theme 3: Help Ontarians Adapt

Strategy #7: Think and plan strategically to prepare for natural disasters and develop and implement adaptation strategies. MNR will sponsor strategic thinking and planning to identify, establish, and modify short- and long-term direction on a regular basis. Accordingly, MNR will work to:

- Strategy 7.A: Sponsor strategic management of climate change issues.
- Strategy 7.B: Maintain and enhance an emergency response capability.
- Strategy 7.C: Develop and implement adaptation strategies for water management and wetlands.
- Strategy 7.D: Develop and implement adaptation strategies for human health.
- Strategy 7.E: Develop and implement adaptation strategies for ecosystem health, including biodiversity.
- Strategy 7.F: Develop and implement adaptation strategies for parks and protected areas for natural resource-related recreational opportunities and activities that are pursued outside of parks and protected areas.
- Strategy 7.G: Develop and implement adaptation strategies for forested ecosystems.

Strategy #8: Ensure policy and legislation respond to climate change challenges. Policy, legislation, and regulation guide development and use of the programs needed to combat climate change. MNR will work to ensure that its policies are proactive, balanced and realistic, and responsive to changing societal values and environmental conditions.

Strategy #9: Communicate. Ontarians must understand global warming, climate change, and the known and potential impacts in order to effectively and consistently participate in management programs and decision-making processes. Knowledge dissemination through life-long learning opportunities that are accessible and current is critical to this requirement. MNR will raise public understanding and awareness of climate change through education, extension, and training programs.

Forecasting the Response to Climate Change of the Major Natural Biotic Disturbance Regime in Ontario's Forests: the Spruce Budworm

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Ontario

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Summary

Predicting the effect of climate change on insect populations is needed to estimate the costs and benefits of protecting forests from potential damage. Outbreaks of forest insects and diseases in Canada cause losses of 80-110 million m^3 of timber per year, or roughly one billion m^3 over a 10-year period. These exceed one-half of harvest rates (which are about 160-180 million m^3/yr). Many of the processes that lead to stand-replacing outbreaks of insect species depend on climate either directly, through reduced survival following extreme weather events, or indirectly through other effects on host trees. Insect pests are thus a major, but consistently overlooked, forest ecosystem component that have manifold consequences to the structure and function of future forests. This study focused on the spruce budworm because it is the dominant abiotic disturbance in Ontario forests. Global climate change may substantially change the frequency and intensity of pest outbreaks, particularly at the margins of host ranges. The consequent shunting of carbon back to the atmosphere rather than to sequestration in forests as biomass may also influence global warming.

This study contributed to better estimation of climate change effects on insect outbreaks and the consequent impacts on carbon sequestration by: validating and analyzing the GIS data of Ontario's forest health survey records for spruce budworm defoliation and synthesizing the results; analyzing and developing models describing climate – insect outbreak relationships for spruce budworm in Ontario; and developing and applying a method for forecasting how climate change is likely to affect the severity and spatial locations of future insect outbreaks. In the first stage, this method was applied to survey records of spruce budworm defoliation in Ontario in combination with the corresponding historical climate records. The frequency with which a site was defoliated was found to be related to tree species composition and climate (i.e., temperature and precipitation at certain times of the year). In the final stage, predictions of future climate were incorporated for forecasting how spruce budworm defoliation in Ontario might be affected by future climate change. In the resulting forecasts, the total area over which defoliation occurred increased because the area expanded northward but changed little in the south. In addition, the most frequent defoliation seemed to occur north of present locations.

Résumé

Prévoir la réaction au changement climatique de la plus importante perturbation biotique naturelle des forêts de l'Ontario: la tordeuse des bourgeons de l'épinette

Il est nécessaire de prévoir l'effet du changement climatique sur les populations d'insectes pour évaluer les coûts de la protection des forêts contre les dommages potentiels et des bénéfices possibles. Au Canada, les flambées épidémiques de maladies et d'insectes dans les forêts causent des pertes évaluées entre 80 et 110 millions de m^3 de bois d'œuvre par année, soit environ un milliard de m^3 sur 10 ans. Ces pertes représentent plus de la moitié des taux de coupes (qui sont d'environ 160 à 180 millions de m^3 par année). Nombre de processus pour remplacer les peuplements après des flambées d'insectes dépendent du climat, directement à cause du taux de survie réduit après des phénomènes météorologiques extrêmes, ou indirectement à cause d'autres effets sur les arbres hôtes. Ainsi, les insectes ravageurs font partie des écosystèmes forestiers, mais leurs effets, qui des conséquences multiples sur la structure et la fonction des forêts futures, sont bien souvent ignorés. La présente étude vise la tordeuse des bourgeons de l'épinette car c'est la perturbation abiotique qui domine dans les forêts de l'Ontario. Le changement climatique mondial peut modifier de façon importante la fréquence et l'intensité des flambées épidémiques de ravageurs, surtout aux limites des aires de répartition des arbres hôtes. Il s'ensuit la libération du carbone dans l'atmosphère plutôt que son stockage dans la biomasse des forêts, ce qui à son tour influe aussi sur le réchauffement climatique.

Cette recherche a permis de mieux évaluer les effets du changement climatique sur les flambées épidémiques d'insectes et les répercussions sur le stockage du carbone par : la confirmation et l'analyse des données SIG de l'inventaire de l'état de santé des forêts de l'Ontario en rapport avec la défoliation due à la tordeuse des bourgeons de l'épinette et l'élaboration d'une synthèse des résultats; l'analyse et la mise au point de modèles décrivant les relations entre le climat et les flambées de la tordeuse des bourgeons de l'épinette en Ontario; la création et la mise en application d'une méthode permettant de prévoir dans quelle mesure le changement climatique affectera possiblement la gravité des flambées d'insectes à venir et la répartition spatiale de la défoliation. Dans un premier temps, la méthode a été appliquée aux données de l'inventaire sur la défoliation par la tordeuse des bourgeons de l'épinette en Ontario, en les combinant avec les dossiers sur les antécédents météorologiques correspondants. Les résultats ont indiqué un lien entre la fréquence de défoliation d'un lieu, la composition des essences et le climat (p. ex. la température et les précipitations à certains moments de l'année). Au dernier stade, des prévisions météorologiques pour l'avenir ont été incorporées pour vérifier dans quelle mesure la défoliation causée par la tordeuse des bourgeons de l'épinette pourrait être influencée par les changements climatiques en Ontario. Les prévisions qui en ont résulté indiquent que la superficie totale touchée par la défoliation avait augmenté parce qu'elle s'étendait plus vers le nord, mais qu'elle avait peu changé dans le sud. De plus, la défoliation semblait survenir plus fréquemment au nord des emplacements actuels.

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Introduction

It is commonly recognized that climate change will affect boreal forest ecosystems through changes in disturbance regimes (Stocks 1991, Price and Apps 1995, Fleming and Candau 1998). This association reflects the fundamental role that disturbances such as harvest, insects, disease and fire, play in forest ecosystem structure and function. In the Canadian boreal biome, forest insects (particularly defoliators) constitute a major disturbance and affect productivity through unrealized growth, tree mortality, and synergetic interactions with other disturbances. As an illustration, the average annual volume of wood lost to insects in Canada estimated during 1982-1987 represents approximately 1.4 times the losses from wildfire and 0.33 times the annual harvest volume (Hall and Moody 1994). In this context, assessing the potential effects of climate change on forest insect disturbances is important. An increase of 5-10°C across North America by the end of the century, as projected by current climate models (Hengeveld 2000), will likely result in significant changes in insect outbreak dynamics in space and time. Uncertainties associated with the magnitude and direction of these changes substantially reduce the reliability of forest management plans, wood supply projections, and pest protection programs.

The spruce budworm (*Choristoneura fumiferana* Clem.) is the most important insect disturbance in Canada's boreal forest (Fleming 2000). The geographical distribution of this insect extends through the boreal zone and south into the cool temperate forests of the Great Lakes - St. Lawrence forest region. The northern boundary is less certain, but heavy defoliation has been reported within 150 km of the Arctic Circle (Volney and Cerezke 1992, Volney and Fleming 2007). During widespread periodic outbreaks, spruce budworm causes considerable tree mortality of its two principal hosts, balsam fir (*Abies balsamea* (L.) Mill.) and white spruce (*Picea glauca* (Moench) Voss). It also causes significant damage to black spruce (*Picea mariana* Mill.) and red spruce (*Picea rubens* Sarg.).

Climate change will likely affect spruce budworm defoliation dynamics both directly through changes in the parameters of the population dynamics and indirectly through feedback and interactions with other species and abiotic factors (Fleming and Candau 1998). Potential direct effects include changes in insect phenology, in the spatial extent of the populations, and in the frequency and duration of outbreaks. Indirect effects comprise changes in the distribution and phenology of host species, in the population dynamics of natural enemies, and in the interaction with other disturbances, particularly fire. In general, research suggests that outbreak frequency and duration will increase with climate change because of the positive effect of temperature increase and drought on insect physiology (Mattson and Haack 1987, Greenbank 1963) and a possible phenological de-synchronization between the spruce budworm and its natural enemies (Fleming 2000).

Williams and Liebhold (1997) predicted potential shifts in the spatial distribution of spruce budworm defoliation and the spruce-fir forest in northeastern and north central United States under temperature increases of 2, 4, and 6°C. Their analysis is based on linear models of the occurrence of defoliation and the distribution of the spruce-fir forest as functions of climatic variables. The models were fitted using historical data. Climate change effects were extrapolated by adding the desired temperature increase to historical climate data. Both models of defoliation and spruce-fir distribution were then run with the new climate data. Williams and Liebhold's models predict a general "thinning" of the spruce-fir forest in the southern part of its distribution resulting in a steady decrease of the total area occupied by this forest type as temperatures increase. Their predictions for spruce budworm defoliation are similar to those for the spruce-fir forest: the models predict a general "thinning" of the defoliation in the southern part of its historical distribution. However, rather than a northward shift of the distribution, the models suggest a progression of the defoliation towards higher elevation.

We present an analysis of potential changes in the distribution of spruce budworm defoliation under climate change in Ontario. Our approach is similar to Williams and Liebhold's in that we use an empirical model that relates defoliation to historical bioclimatic variables, and then apply climate change data to this model to predict potential changes in the distribution of defoliation. However, some key aspects of the methods and data used to develop our predictions differ from those used in previous work.

Data and Methods

In a recent study, Candau and Fleming (2005) developed empirical bioclimatic models of the spatial distribution of spruce budworm defoliation in Ontario. These models were calibrated using defoliation data from the most recent spruce budworm outbreak in Ontario (1967-1998) and bioclimatic data for approximately the same period. We estimated potential changes in the distribution of budworm defoliation under climate change by applying climate forecasts to the bioclimatic models. Since the error associated with climate forecasts and with the knowledge of how complex ecosystems will react to climate change likely increases with the time into the future, we limited our study to the period 2002-2033. Under the assumption that large-scale budworm defoliation in Ontario will follow the same temporal pattern observed during the 20th century (Candau et al. 1998), we estimated that this period would approximately correspond with the next spruce budworm outbreak.

Bioclimatic model of the spatial distribution of spruce budworm defoliation

Candau and Fleming (2005) developed two empirical bioclimatic models of the spatial distribution of spruce budworm defoliation in Ontario. Both models relate the distribution of defoliation to various environmental variables such as climate (temperature and precipitation), forest age structure and composition, and elevation. The models were calibrated using historical data. Spruce budworm defoliation data consisted of the frequency of moderate-to-severe defoliation recorded during extensive, annual aerial surveys since 1941. The models, however, were constructed on a subset of these data for the period 1967-1998, corresponding to the most recent outbreak (Fig. 1).

Figure 1. *Cumulative frequency of moderate to severe defoliation in Ontario from 1967 to 1998. The key indicates the number of years defoliation was recorded. Areas with the highest frequencies of defoliation ("hot spots") are grouped in three zones (Lac Seul, Lake Nipigon, and Algoma) separated by two corridors of less frequent defoliation. Dashes outline the area for which forest composition data are available.*

Lac Seul   Lake Nipigon   Algoma

1-3 years
4-6 years
7-9 years
10-12 years
13-19 years
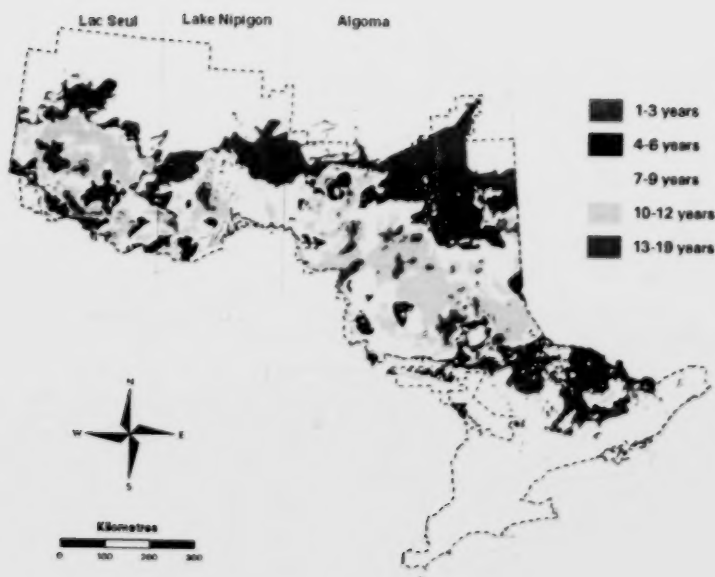
Climate variables, based on normals for the period 1961-1990, included composite values that reflect the phenology of spruce budworm such as winter (Dec.-Feb.) mean minimum and mean maximum temperatures, spring (Mar.-May) mean minimum temperature, summer (May-Aug.) mean minimum and mean maximum temperature, and summer mean precipitation. In addition, monthly minimum and maximum temperature during the feeding and adult periods (i.e., from May to August) were included in the analyses. Forest age structure data consisted of a proportion of the forested area occupied by each 20-year age class in each cell of a grid of variable size (ranging from 5×5 to 10×10 km). Forest composition data were based on the same grid and limited to two variables related to spruce budworm: the proportion of forested area covered by the main host species (balsam fir and white spruce) and the proportion of forested area covered by common host species in Ontario (balsam fir, white spruce, and black spruce). Both of the models developed by Candau and Fleming (2005) use the regression tree analysis method, a form of multivariate analysis that involves successively partitioning a data set into increasingly homogeneous subsets. Regression tree analysis provides a flexible alternative to linear and additive models when non-linear and non-additive relationships are expected and when the relationships between the response variable and some predictor variables are conditional on the values of other predictors. The first model applies to the presence/absence of defoliation during the period 1967-1998 (Fig. 2). It relies on 3 variables to predict the occurrence of defoliation: the proportion of balsam fir, the maximum winter temperature, and the minimum temperature in May. Overall, the model performs well, with a misclassification error rate of 0.15.

The second model relates to the frequency of defoliation during the same period (Fig. 3). The model uses 5 variables associated with temperature (minimum and maximum winter temperature, minimum spring temperature, maximum temperature in May, and minimum temperature in August), two variables related to forest composition (the proportion of balsam fir and white spruce and the proportion of balsam fir, white spruce, and black spruce) and one variable related to precipitation in May. This model performs fairly well when applied to independent data: in 80% of the cases the error rate in the estimate of the frequency of defoliation during the period 1967-1998 is less than 10%. However, the model cannot predict the highest class of frequency defoliation (above 13 years) and thus underestimates the frequency of defoliation in areas where defoliation is the most frequent (i.e., "hot spots" shown in Fig. 1).

Figure 2. Fitted regression tree for the presence/absence of moderate-to-severe spruce budworm defoliation in Ontario, 1967-1998. Ovals and rectangles represent the tree's nodes and terminal leaves, respectively, and contain the corresponding predicted values (with 1 indicating presence and 0 indicating absence of defoliation). Misclassification error rates can be calculated from the numbers of cases with/without defoliation (shown in parentheses). Each partition is represented as an inequality involving one of the variables: FbSw, the proportion of the area covered by balsam fir and white spruce; TmaxWinter, the maximum winter (Dec.-Feb.) temperature (°C); and MINT5, the minimum May temperature.

7.2
n=591

TminWinter<-23.3
TminWinter≥-23.3

2.1
n=120

7.9
n=471

TmaxWinter<-11.0
FbSwSb<0.143

TmaxWinter≥-11.0
FbSwSb≥0.143

2.1
n=50

5.9
n=70

5.9
n=74

8.3
n=397

FbSw<0.069
TmaxWinter<-11.6

FbSw≥0.069
TmaxWinter≥-11.6

4.6
n=40

7.7
n=30

3.3
n=15

8.5
n=382

TminWinter<-22.2
TminWinter≥-22.2

7.2
n=105

9.0
n=277

MINT8≥8.9
MAXT5≥17.9

MINT8<8.9
MAXT5<17.9

5.9
n=47

8.2
n=58

4.4
n=12

9.2
n=265

PCP6≥86.0
PCP6<86.0

8.8
n=203

10.0
n=62

TminSpring≥-2.7
TminSpring<-2.7

7.5
n=13

11.0
n=49

Fig. 3. *Fitted regression tree of the frequency of moderate-to-severe spruce budworm defoliation in Ontario, 1967-1998. Ovals and rectangles represent the tree's nodes and terminal leaves, respectively, and contain the corresponding predicted frequencies and sample sizes. Each partition is represented as an inequality involving one of the variables: TminWinter, the minimum winter (Dec.-Feb.) temperature (°C); TmaxWinter, the maximum winter temperature; FbSw, the proportion of the area covered by balsam fir and white spruce; FbSwSb, the proportion of the area covered by balsam fir, white spruce, and black spruce; MINT8, the minimum Aug. temperature; MAXT5, the maximum May temperature; PCP6, the precipitation (mm) in June; and TminSpring, the minimum spring (Mar.-May) temperature.*

Climate projections

Climate projections were derived from historical climate normals by adding a constant to represent the effect of climate change (by adding 4°C to the normals related to temperature). However, this approach does not account for any spatial heterogeneity or any seasonal variations in the effects of climate change. Thus, we tried to account for these factors by adding spatially and temporally explicit, predicted values of climate change effects to historical climate normals. The climate normals for the period 1961-1990 were obtained from the spatial interpolation of monthly climatic variables from 471 meteorological stations (Price et al. 2000). These normals are identical to those used to develop the bioclimatic models of defoliation. The predicted values of climate change effects were obtained from the Canadian Global Coupled Model (CGCM1) (Flato et al. 2000). This model uses an atmospheric circulation model coupled to an ocean circulation model and a greenhouse gas forcing scenario of 1% per annum increase in atmospheric CO_2 equivalent concentration. The model produces grids for a variety of monthly averaged climatic variables for every year from 1900 to 2100 at a spatial resolution of approximately 270×415 km. We calculated the climate change predictions for the period 2002-2033 for each variable used in the bioclimatic models of defoliation. For each variable, predictions were established by following a 3-step process: (1) we

calculated the differences between CGCM1 predictions for the period 2002-2033 and CGCM1 predictions for the baseline period 1961-1990; (2) the resulting grid was scaled to the resolution of the historical climate normals (1 km) using a 3rd-order linear interpolation; and (3) the differences were then applied to the corresponding climate normals. Depending on the variable, predictions for the period 2002-2033 indicate a temperature increase of 1.3 - 4.0°C (Table 1). In contrast, the change in June precipitation is not significant.

Table 1. Averages of historical normals and predicted changes for 7 climatic variables in Ontario. Historical normals (1961-1990) are based on records from 471 meteorological stations across Ontario interpolated on a 1-km grid Predictions (2002-2033) are based on the Canadian Global Coupled Model (CGM1) (Flato et al. 2000) scaled to the same 1-km grid.
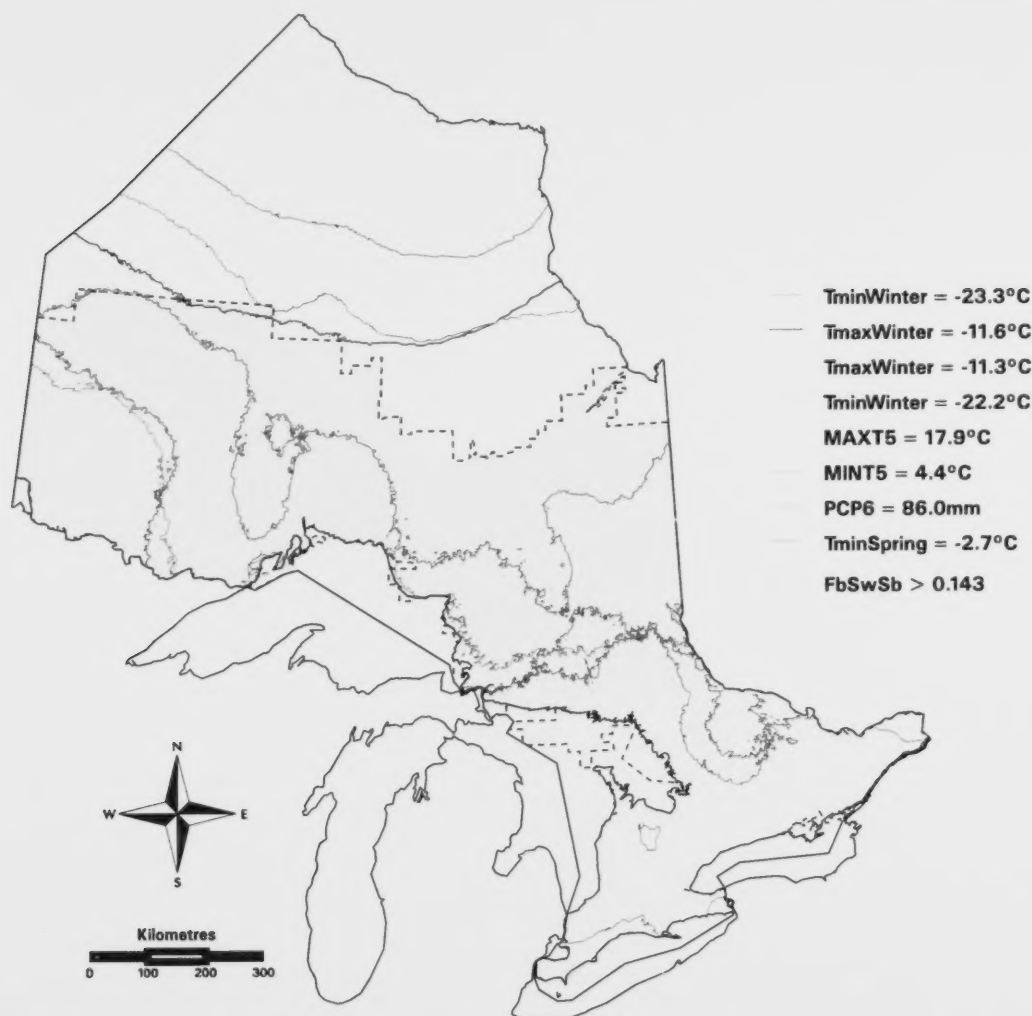
Climate variable[1]	Period		Difference between historical average and predicted
	1961-1990 (historical average)	2002-2033 (predicted)	
TminWinter (°C)	-22.6	-18.6	+4.0
TmaxWinter (°C)	-11.2	-8.8	+2.4
TminSpring (°C)	-7.2	-5.4	+1.8
MINT5 (°C)	1.3	2.6	+1.3
MAXT5 (°C)	13.9	15.5	+1.6
MINT8 (°C)	9.5	11.1	+1.6
PCP6 (mm)	79.3	79.4	+0.1

[1] Where, TminWinter = the minimum winter (Dec.-Feb.) temperature (°C); TmaxWinter = maximum winter temperature; MINT5 = minimum May temperature; MAXT5 = maximum May temperature; MINT8 = minimum Aug. temperature; PCP6 = precipitation (mm) in June.

Results

The effects of climate change on the frequency of defoliation were assessed by applying climate forecasts for the period 2002-2033 to the bioclimatic models. Ultimately, model output (presence/absence) was combined with the results of the frequency model to produce a projected map of defoliation. The projected map of defoliation was compared to the map of observed defoliation prepared for the last outbreak (1967-1998) and to the predicted map of the output of the bioclimatic model based on 1961-1990 climate data.

Because of the northward movement of the isotherm TmaxWinter (-11.3°C) (Fig. 4), a substantial increase in defoliation is forecast for the north. These forecasts (Fig. 5) are based on combining projections of where defoliation is likely to occur with projections of how often defoliation is expected to occur in those locations during the forecast period.

TminWinter = -23.3°C

TmaxWinter = -11.6°C

TmaxWinter = -11.3°C

TminWinter = -22.2°C

MAXT5 = 17.9°C

MINT5 = 4.4°C

PCP6 = 86.0mm

TminSpring = -2.7°C

FbSwSb > 0.143

Figure 4. Predictions of the location of some isotherms in a climate change scenario for the period 2002-2033. These isotherms correspond to the partitions retained in the regression tree models of presence/absence (Fig. 2) and frequency (Fig. 3) of moderate-to-severe spruce budworm defoliation in Ontario. The partitioning variables are TminWinter, the minimum winter (Dec.-Feb.) temperature (°C); TmaxWinter, the maximum winter temperature; MAXT5, the maximum May temperature; MINT5, the minimum May temperature; PCP6, the precipitation (mm) in June; TminSpring, the minimum spring (Mar.-May) temperature; and FbSwSb, the proportion of the total area covered by balsam fir, white spruce, and black spruce. Forest composition data are not available north of the dashed line.

Considering the short timeframe of our forecasts (2002-2033), it was assumed that the proportions of balsam fir and white spruce (BfSw) would remain similar to present values even in a slightly different climate. Consequently, the southern limit of the defoliation associated with BfSw remains identical. Inside the predicted defoliation belt, patterns of defoliation frequency appear considerably different from historical patterns. In the southeast and southwest, areas of low-to-medium frequencies (4 to 6 years) cover the areas of low-to-medium frequencies observed on the historical map (Fig. 1) and extend north of these areas. In the Lac Seul area of Northern Ontario, the area of low-to-medium frequencies observed in the southwest corner on the historical map (Fig.1) has increased due to the migration northward of the isotherm MAXT5 (17.9°C). This area also contains
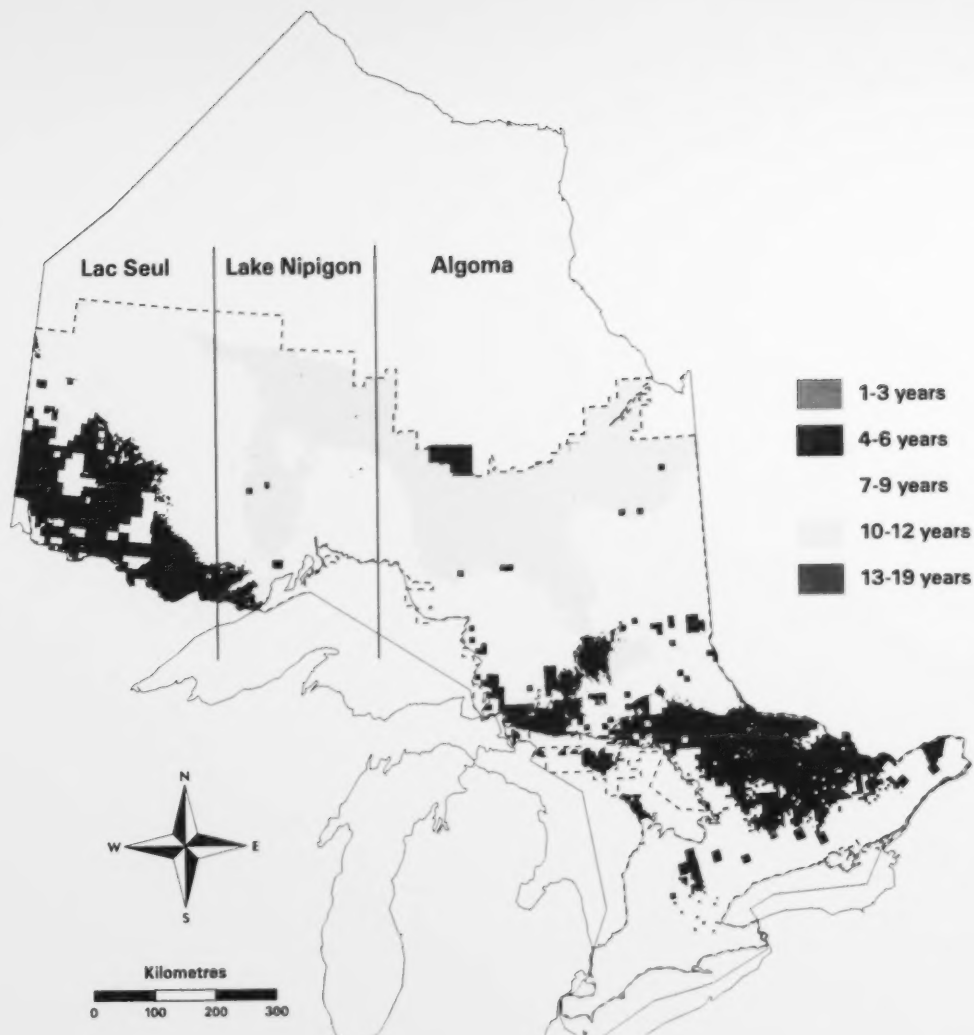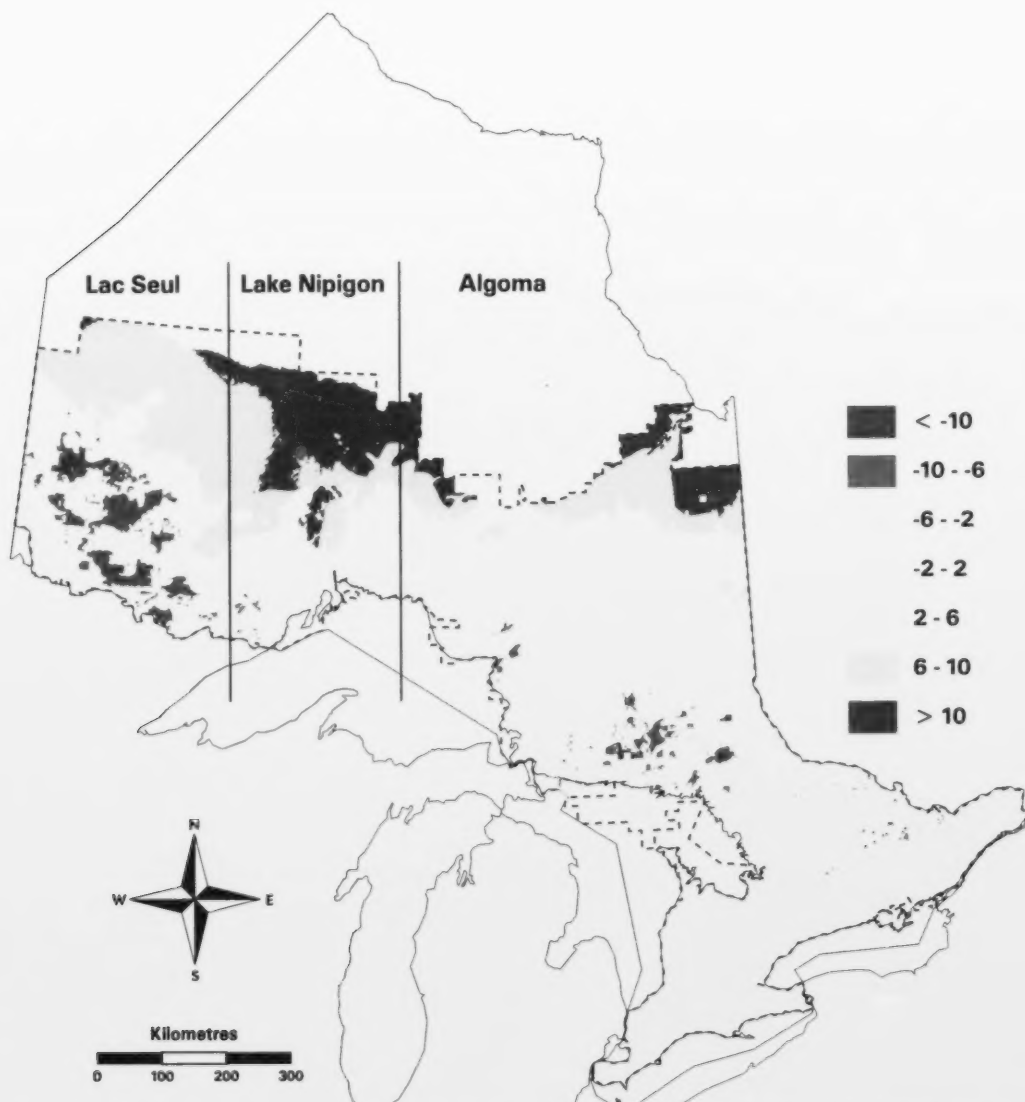
Figure 5. Expected frequency of defoliation during a 32-year period as predicted under climate change. The frequency of defoliation was predicted, for each cell of a grid at 1-km resolution, using a regression tree model (Fig. 3) and climate forecasts for the period 2002-2033 (Fig. 4).

pockets where the defoliation frequency under climate change is estimated to be 0; these pockets are areas where BfSw < 0.0458 (i.e., less than 4.58% of the area supports balsam fir and white spruce) that are not defoliated in our forecast because of the northward migration of the isotherm MINT5 (4.4 °C). An area of medium frequencies (7 to 9 years) extends in the northwest beyond the observed northern limit of defoliation, in the centre of the defoliation belt, and in the east. Finally, an area of medium-to-high frequencies (10 to 12 years) covers the northern part of the defoliation belt, extending the limit of defoliation northward to the limit of available data. Areas of low frequencies (1 to 3 years) are missing because, under the climate scenario used in this study, the isotherm associated with the southern limit of these areas (TminWinter = 23.3 °C) has moved northward beyond the limit of the study area. Likewise, areas of high frequencies (13 to 19 years) of defoliation are absent because the highest frequency output by the regression tree model is 11.0.

The differences between projected and observed frequencies (Fig. 6) emphasizes higher frequencies of defoliation in the northern part of the study area due to the emergence of new areas of defoliation, particularly in the Lake Nipigon area, and an increase in areas with low historical frequencies. Conversely, some areas show a decrease of frequency, prominently in the Lac Seul area and in the centre of Algoma. A part of this decrease is explained by the inability of the regression tree model to predict high frequencies of defoliation. A comparison between predicted frequencies using historical climate data and predictions using climate change data (Fig. 7) confirms the decrease in frequency in the Lac Seul and Algoma areas and the increase of frequencies in the north of the study area.

Figure 6. *Differences between predicted frequency of defoliation under climate change (2002-2033) and historical values (1967-1998). Blue and green shades indicate a decrease while yellow and red shades indicate an increase in frequency.*
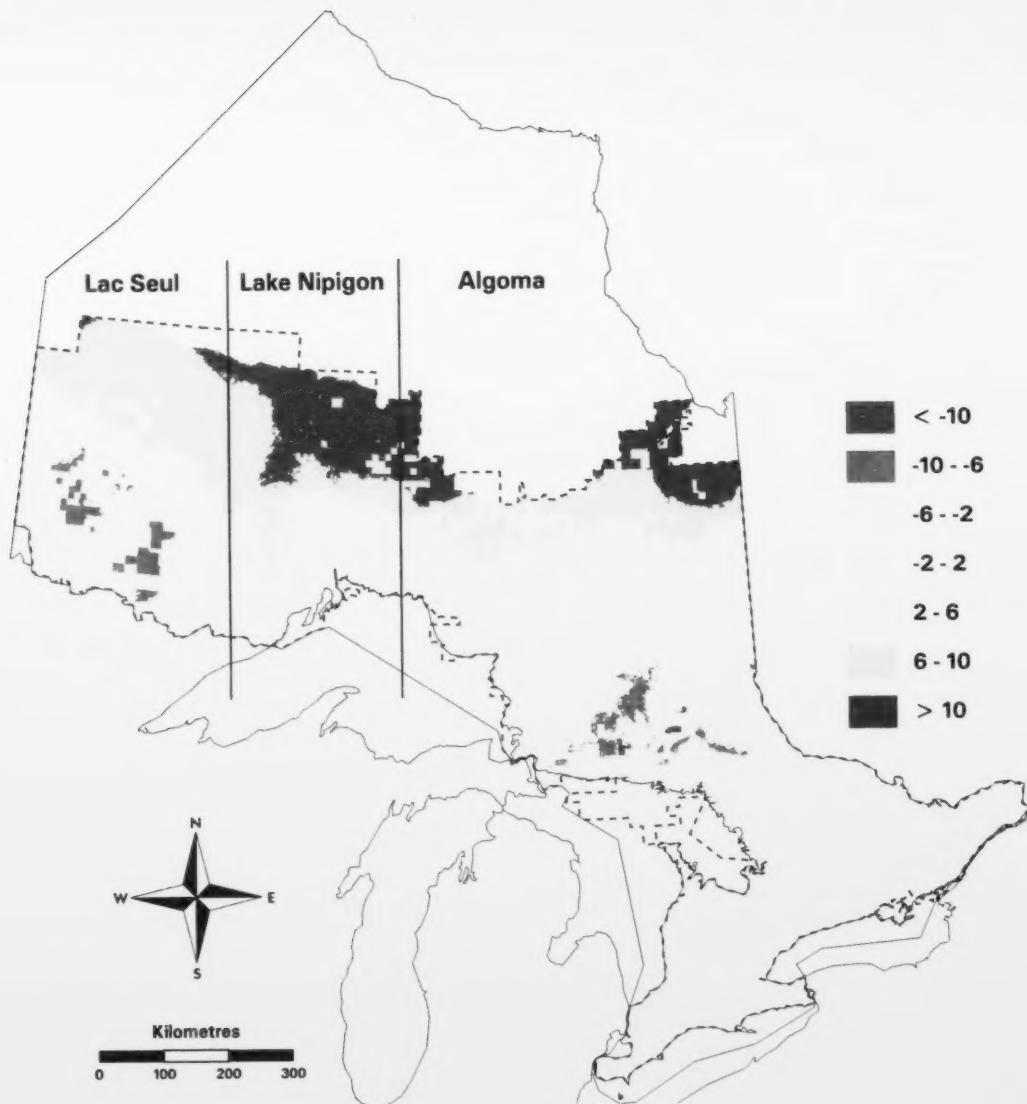
Figure 7. *Differences between values of the frequency of defoliation predicted by a regression tree model using climate data under a climate change scenario and estimates of the frequency of defoliation based on the same regression tree using historical bioclimatic data. Blue and green shades indicate a decrease while yellow and red shades indicate an increase in frequency.*

Discussion

A defoliation event is the result of the spatiotemporal dynamics of a spruce budworm population and the simultaneous presence of host species. Both of these elements are likely to be affected by climate change as well as their interrelations, and their interactions with each other, other species and abiotic components of their habitat. For instance, it is expected that the combined effects of climate warming and CO_2 fertilization will directly affect spruce budworm populations through an increase of individual growth rate (Lysyk 1989), survival (Lucuik 1984) and fecundity (Sanders et al.1978). The resulting increase in the population's net per capita growth rate could be reduced by competition among individuals of the same generation and trophic interactions with other species in the food-web. Competitive interactions between insects of the same generation, however, appear significant only among feeding larvae at high densities (Sanders 1991). Therefore, it is expected that trophic interactions will be the principal modifiers of the relation between climate change and per capita growth rate of spruce budworm populations (Fleming 1996). According to Royama (1992), local budworm population dynamics are largely driven by a complex of density-dependent mortality agents including parasitoids and diseases. Climate change will almost certainly affect the population dynamics of at least some of these agents and their phenological synchronization with budworm. However, because it is likely that each agent will be affected differently and that their interrelations could also be affected, the net result of climate change on this complex of regulatory factors is largely unknown and difficult to predict (Fleming 1996).

Host species distribution may be modified by climate change. Weather variables such as temperature, precipitation, and wind will affect the vegetation in association with other factors such as soils and terrain. Several researchers forecast a northward shift of balsam fir leading to almost complete removal of the species from the north central and northeastern United States (Iverson et al. 1999, Williams and Liebhold 1997). It is reasonable to expect that a northward shift of balsam fir will also occur in Ontario, decreasing the balsam fir component in the south and increasing it in the north. Climate could also exert indirect influences on host species distributions through the frequency and severity of disturbances such as fire on habitat. For example, fire frequency may decrease under climate change because an increase in precipitation could more than compensate for the increase in temperature (Bergeron and Archambault 1993, Flannigan et al. 1998). In northern Ontario, a decrease in fire frequency would likely lead to an increased abundance of shade-tolerant species such as balsam fir and white spruce.

The phenology of spruce budworm is synchronized with the phenology of its host to provide developing, rather than mature, foliage to the larvae when nutritional needs are greatest. Developing foliage offers low fibre (which improves digestibility), high nitrogen (necessary for insect growth), and low secondary metabolites (host defensive chemicals). Climate change could potentially disrupt the phenological synchrony between the pest and its host. However, simulations of the phenological development of the spruce budworm and comparisons with the phenology of white spruce (Volney and Cerezke 1992) and balsam fir (Régnière and You 1991) have shown that the insect is so well synchronized with its hosts that a disruption of this synchrony under climate change is relatively unlikely.

Our projection of the distribution of the frequency of spruce budworm defoliation for the period 2002-2033 shows significant change from distributions of the recent past. The model suggests a northward expansion of the defoliation belt to a limit corresponding either to the limit of balsam fir and white spruce distributions or, especially in the northwest, beyond the limit of available vegetation data. Overall, the area defoliated increases because minimal simultaneous disappearance of defoliation is predicted in the south, especially compared to that predicted in north central and northeastern United States (Williams and Liebhold 1997). Our predictions also show a latitudinal gradient in defoliation frequency: areas of medium-to-high frequencies are limited to the northern portion, medium frequencies are in the centre, and low-to-medium frequencies occur in the south. However, in the north, the artificial limitation of the defoliation due to the absence of vegetation data prevents a complete picture

of the predicted distribution of defoliation. In particular, we are not able to assess if the projected distribution corresponds to a simple northward shift of historical distribution or if climate change will induce a complete change in defoliation patterns.

As mentioned above, our models do not predict the disappearance of the defoliation in the southern part of the belt as predicted for the north central and northeastern United States (Williams and Liebhold 1997). This difference is due to the fact that we assumed that host species will remain at the southern limit of defoliation during the next outbreak and that the warmer temperatures predicted during this period will remain in the "acceptable" range for spruce budworm.

Approaches to characterizing how individual components of an ecosystem will be affected by climate change differ (Fleming 1996). In the integrated approach, species assemblages move as complete units following the northward shift of climatic zones. In this case, the geographic distribution of pest damage may incur a latitudinal shift, but the overall effect (in terms of volume losses per unit area) should not change substantially.

Alternatively, in an individualistic approach, species or even certain age classes of the same species, move individually at different rates and possibly at different locations. This individualistic approach can be illustrated by the simple dynamic model of spruce budworm-balsam fir interactions derived by Antonovsky et al. (1990) and used in a mechanistic assessment of the effects of climate change on the spruce budworm-balsam fir complex (Fleming 1996). In this theoretical model, the spruce budworm-balsam fir system can experience four qualitatively different long term behaviours depending on the ratio of tree senescence to regeneration (see Fig.1 in Fleming 1996). As this ratio increases, the different long term behaviours are characterized as: stable equilibrium (SE in Fleming 1996), insect and host persistence (or extinction) if tree densities are above (or below) a certain threshold (Tt), insect extinction and tree persistence (or extinction) if tree densities are above (or below) a certain threshold (Ttlx), and system extinction (SX). Consider the assumption that each of these dynamics would translate into a different pattern of defoliation frequencies. Then, the stable equilibrium would likely be associated with the central area of defoliation. In this area, the defoliation frequencies are medium to high and host species are present almost everywhere. The next type of dynamics, Tt, would then correspond to defoliated areas located outside the above-mentioned area. In these areas, defoliation frequencies are low and host species are sparser. The regression tree model of presence/absence of defoliation (Fig.2) indicates that defoliation occurs in these areas only when the proportion of host species is above a threshold (e.g., BfSw >0.04 or 4%). A parallel can be made between this threshold and the threshold based on the ratio of tree senescence to regeneration in the Antonovsky et al. (1990) model. The third type of dynamics would then match areas outside the defoliation belt where host species are present. This portion of the host species range is exempt from defoliation severe enough to be detected by forest insect and disease aerial surveys in the model. Finally, the extinction type dynamics would correspond to areas outside the host species range.

Under climate change, it is expected that warmer temperatures will increase seedling mortality (and therefore decrease regeneration) comparatively more than it will increase the senescence of established trees in the southern part of the host species range. Consequently, age-class distributions will be shifted towards older classes as seedlings progressively "move" northward before established trees do (as well as before the budworm does since it "prefers" older trees). As the ratio of senescence to regeneration increases, areas in what might be termed "stable equilibrium" will move to the next state, Tt. In this state, insect and host are present because host densities are still above the threshold due to the survival of established trees. As the warming continues, however, the host densities will not sustain spruce budworm populations and areas in state Tt will move to state Ttlx for which the insect is extinct but the host is still present because densities remain above the threshold. This situation corresponds to the Williams and Liebhold (1997) scenario where pockets of host trees persist but are not adequate to sustain sizeable spruce budworm defoliation. Eventually, further warming will increase the ratio of senescence to regeneration to a state SX during which the spruce budworm-fir-spruce system gradually becomes extinct and is replaced by another type of ecosystem (e.g., deciduous forests, shrubs, or grassland) altogether.

In the northern part of the host species range, climate warming will decrease the ratio of senescence to regeneration and sites will become progressively more suitable to the host and the insect. However, areas may evolve differently depending on their starting point (Fleming 1996). On a site which did not previously contain host species (SX state), increasing temperatures will move the site to a Ttlx state and then to Tt, but at this point the site will still have relatively few host trees and spruce budworm outbreaks will be very rare (in contrast to southern sites, not enough trees are established on this site to keep the densities above the threshold). Large numbers of host trees and insect outbreaks appear only when climate warming decreases the ratio of senescence to regeneration to a point where the site is in a stable equilibrium. On a site that previously contained host trees but no insect (state Ttlx), climate change can shift the site to a state Tt where host trees (because densities remain above the threshold) as well as the insect will occur. Further warming can create a stable equilibrium. Thus, the model suggests that two sites that have evolved to an identical state Tt, may experience two alternative, qualitatively different situations (local extinction versus maintenance of the forest-pest system) depending on their recent history.

The behaviour of the spruce budworm-balsam fir complex under climate change predicted by Antonovsky et al.'s (1990) model can be compared to the regression tree predictions. Such comparison is limited by the fact that the regression tree model is deterministic and does not include changes in host species distribution. For short-term predictions (e.g., up to 2033), however, it is not expected that these models would diverge much. In the southern part of the defoliation belt, the regression tree model predicts that areas of low-to-medium frequencies of defoliation will remain the same. This prediction agrees with Antonovksy et al.'s (1990) model, which predicts that these areas will evolve slowly because the densities of established trees are far above the threshold of extinction. In the longer term, however, these areas are predicted to move towards a Ttlx state as host densities decrease and ultimately enter the state of extinction of the system.

In the central part of the defoliation belt, the regression tree model predicts that some areas will remain at medium-to-high frequencies whereas in some areas the frequencies will decrease to low-to-medium. Antonovsky et al.'s (1990) model predicts that areas experiencing a stable equilibrium (SE) will move to a threshold-dependant state (Tt), but in most places this threshold will be exceeded because of the presence of established trees. In the longer term, these sites are expected to shift towards a Ttlx state and ultimately lead to extinction of the system.

In the northern part of the defoliation belt and beyond the northern limit, the regression tree predicts a dramatic increase of the frequencies of defoliation from none or low-to-medium to medium-to-high. Antonovsky et al.'s (1990) model identifies two different situations in this case: (1) On sites where the host species is present and above or close to the threshold, the dynamics are predicted to move from Ttlx to Tt and SE as established trees are maintained, senescence is decreased, and regeneration is increased. In the model, host densities remain above the threshold and defoliation appears quickly. (2) On sites where host trees are initially rare, tree senescence is expected to decrease and tree regeneration to increase, but modelled host densities take a long time to reach the threshold at which defoliation first appears.

Our study is based on an inductive approach in which the relationship between climate and defoliation are inferred from observed distributions and on the premise that these will hold under climate change. Several difficulties are associated with this approach (Sutherst et al. 1995), including the uncertain role of climate in determining the distribution of defoliation and the degree of model fitting that limits the explanatory capacity of the model. However, an attempt was made to limit these difficulties by choosing the variables included in the analysis based on biological relevance. In addition, the equilibrium approach is limited.

Antonovsky et al.'s (1990) results suggest that an inductive approach may not be suited for longer term predictions when the system can evolve differently depending on its dynamics, past history, and stochastic events. Therefore, dynamic, spatially explicit models of the spruce budworm-balsam fir complex will need to be developed to improve the reliability of longer term predictions.

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